Fire History and Soil Gradients Generate Floristic Patterns in Montane Sedgelands and Wet Heaths of Gibraltar Range National Park

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High rainfall escarpment areas along the Great Dividing Range provide habitats for sedgeland and wet heath vegetation in areas with impeded drainage. There are few studies of the processes that influence the floristic composition of montane sedgelands and heaths in relation to fires that sweep these landscapes. Gibraltar Range National Park contains extensive areas of sedge-heaths that remain mostly free from anthropogenic disturbance. These areas have a well-known fire history which provides an opportunity to test whether: 1) plant resources are related to time-since-fire; 2) floristic composition is more strongly related to physiographic factors than time-since-fire, and 3) floristic composition of vegetation is related to fire frequency. Physiographic position strongly influenced the vegetation's structure and floristic composition, with taller heaths confined to better-drained edges whereas sedgelands were more common in poorly drained slopes regardless of fire regime. In turn, these patterns were related to soil conductivity reflecting the fertility status of the soils. Upper slope heaths were more species rich than those lower in the landscape where soil conductivity was higher. Time-since-fire strongly influenced heath structure and species richness declined in the heaths with canopy closure at some sites. Floristic composition across the physiographic gradient was more divergent soon after fire and became more similar 15 years after fire. Fire frequency had no significant effect on shrub species richness, but frequent fires decreased the abundance of some woody species. Inter-fire intervals of less than seven years may reduce the abundance of some shrub species. Both the history of fire and ease of access make the sedgelands and wet heaths of Gibraltar Range an ideal location to assess the long-term effects of fire regimes in montane sedge-heaths.

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KEYWORDS: Fire ecology, heaths, resource gradients, species richness, time-since-fire.

INTRODUCTION

Montane plateaux along the Great Dividing Range have high rainfall and low evaporation creating ideal conditions for sedgelands and wet heath communities where drainage is impeded (Keith 2004). Beadle (1981) described the mosaic of sedgelands and wet heaths as "sedge-heaths", but more recently Keith (2004) has circumscribed them as "Montane Bogs and Fens", reserving the term "Montane Heaths" to those heathlands with well-drained soils on rocky sites. The more poorly drained sedgelands are dominated by species of the monocotyledon families Cyperaceae, Juncaceae and Restionaceae whilst adjacent wet heaths are dominated by shrubs, especially of the families Ericaceae, Fabaceae and Myrtaceae (Keith 2004).

The earliest studies of sedge-heaths identified that sedgelands dominated the wettest areas, while shrubs were more common in better-drained positions (Pidgeon 1938). Early descriptions also considered sedge-heaths as a sere in succession leading to more complex vegetation (Pidgeon 1938; Davis 1941; Jackson 1968). With this focus, Millington (1954) was the first to describe the sedge-heaths of the Northern Tablelands of NSW describing the cyclic formation of *Sphagnum* hummocks and hollows following

the European tradition. More recently, Whinam and Chilcott (2002) surveyed the floristic composition and environmental relationships of *Sphagnum* bogs in eastern Australia but did not sample those areas where *Sphagnum* was absent.

Contemporary studies have considered geology, soil depth and soil moisture as interrelated factors controlling floristic patterns within sedge-heath communities (Burrough et al. 1977; Buchanan 1980; Brown and Podger 1982; Pickard and Jacobs 1983; Bowman et al. 1986; Myerscough and Carolin 1986). The importance of water level in determining the distribution of dominant montane sedge-heaths species was shown by Tremont (1991), who evaluated the effects of hydrological changes resulting from a dam built across a wet heath in Cathedral Rock National Park. Resource-driven processes were highlighted in the detailed studies of Keith and Myerscough (1993) who found species richness was inversely related to soil resources, consistent with resource competition models that predict greatest species diversity with lowest levels of resources (Tilman 1982).

Fire is a regular event in sedge-heath communities, due to the dense graminoid biomass and the fine elevated fuels presented in the leaves of the sclerophyllous shrubs. Both obligate seeder (fire-killed) and resprouting species co-exist within wet heaths, although resprouting shrub species are more numerous than those killed by fire (Clarke and Knox 2002). Plant species richness is usually highest in the initial post-fire community, due to the recruitment of short-lived species (e.g. Specht et al. 1958), with an inverse relationship between shrub canopy cover and understorey species richness (Specht and Specht 1989; Keith and Bradstock 1994). Frequent fires in sedge-heath communities also have the potential to alter floristic composition if the life cycles of plants are not completed between fire intervals (Keith et al. 2002).

There are few studies of the processes that mediate the floristic composition of the montane sedge-heaths in northern NSW, unlike their coastal and southern counterparts (see Keith 2004). Gibraltar Range National Park contains extensive areas of montane sedge-heaths that remain mostly free from anthropogenic disturbance. These bogs and heaths also have a well-known fire history which provides an opportunity to test whether: 1) plant resources (soil and light) are related to time-since-fire; 2) floristic composition is more strongly related to physiographic factors than time-since-fire, and 3) floristic composition is related to fire frequency.

MATERIALS AND METHODS

Study sites

Study sites were located in Gibraltar Range National Park in February 1995 by choosing replicate sedge-heaths that were widely spaced with different fire histories. Fire histories of different sections of the park were determined through consultation with park staff and their fire history records. Fire frequency over the last 30 years was found to be similar for many sedge-heaths of the park, differing only in whether they had been burnt since 1980 (i.e. differing in the time since last fire).

Sedge-heaths occur as distinct swampy low-lying islands surrounded by eucalypt forest. Six sedge-heaths were selected for this survey based on certainty and differences in known fire history and ease of access. All six sedge-heaths were burnt in wildfires of both 1964 and 1980. Two remained unburnt since 1980 and were considered in this study as long unburnt (i.e. 15 years since fire). Two sedge-heaths were burnt in a planned burn in 1994 and were considered regenerating communities, having been burnt only half a year prior to this study. The remaining two sedge-heaths had an intermediate age since last fire. One was burnt in a wildfire in 1989, the other in a planned burn in 1990. Therefore of the six sedge-heaths surveyed, two were last burnt 15 years, two 5-6 years, and two were burnt half a year prior to the survey (Williams 1995). Following the 1995 survey all study sites were burnt by a landscape-scale wildfire seven years later in November 2002 and a subset of the original sites were re-sampled.

Sampling design

Preliminary inspections of the sites suggested that floristic patterns were likely to vary with the soil moisture gradient from the drier outer edge to the drainage channels flowing through the centre of each sedge-heath, as documented in similar communities in southern Australia (e.g. Buchanan 1980; Keith and Myerscough 1993). Therefore a stratified sampling design was used, where each sedge-heath was divided into three habitats: drier outer edge, mid-slope and drainage channel. To survey spatial variation, three plots were placed in each of the three habitats in each of the top, central and lower sections of sedge-heath. Therefore 27 plots (3 habitats x 3 plots x 3 sections) were surveyed in each of the six sedge-heaths (2 areas x 3 time-since-fire), providing a total of 162 plots. In addition 36 plots (2 habitats x 3 plots x 2 areas x 3 fire frequencies) were re-sampled in 2003 for woody species. In this sampling, the drier outer edge and

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drainage channel were surveyed in each of two sedge-heaths for each fire frequency.

The quantitative nested quadrat method (Morrison et al. 1995) was used to document species abundance at each plot. This method uses concentric sub-quadrats of increasing size, which were 1, 4, 9, 16 and 25m^2 in this study. An abundance score out of five was given to each of the species at each plot, derived from the number of sub-quadrats it was present within. Plant nomenclature follows Harden (1990-93) with later modifications adopted by the National Herbarium, Sydney, and voucher specimens of uncommon species were lodged in the NCW Beadle Herbarium (NE) Herbarium. Fire responses (obligate seeder or resprouter) were documented for species within the recently burnt sites. Electrical conductivity and soil pH measurements were taken using electronic meters and a 1:5 ratio of soil to distilled water. Electrical conductivity is positively correlated with soil ionic concentrations and hence is a crude index of soil fertility. A light reading was taken at the soil surface at each plot and calculated as a percentage of a reading taken above the canopy. Aspect, degree of slope and canopy height were also recorded at each plot.

Analyses

The species composition and abundance data for each plot were correlated with environmental variables using a canonical correspondence analysis (CCA) through the CANOCO program. The CCA is calculated in two stages. Firstly the similarity of the 162 plots, based on species composition and abundance, is calculated to display the relative ordering of sites (i.e. ordination). The ordination is undertaken using a correspondence analysis (CA), which is a modal response model, which assumes species reach a maximum abundance at a point along an environmental gradient. The second step in the CCA is a multiple regression technique that evaluates the link between environmental variables at each plot and the initial ordination of plots based on species abundance. In addition, the 36 plots (2 habitats x 3 plots x 2 areas x 3 fire frequencies) that were re-sampled in 2003 for woody species only were analysed using CCA with fire frequency and habitat as environmental variables.

The relationships between environmental variables of canopy height, light, pH and soil conductivity, and habitat and time-since-fire were examined using a general linear model (GLM) with habitat (3 levels) and time-since-fire (3 levels) as orthogonal factors. This orthogonal design was also applied in GLM analyses for the richness response variables of total species, resprouters, obligate seeders, woody plants, graminoids, grasses, ferns and forbs. In addition analyses of covariance were performed with conductivity as a covariate. A fire-frequency orthogonal GLM analysis was also applied to species richness data collected in 2003 with fire frequency (3 levels) and habitat (2 levels). A Poisson error structure with a log link function was applied for species richness data, a binomial error structure with a logistic link function for species presence/absence data and an identity link function was applied to normally distributed data.

RESULTS

Effects of time-since-fire and habitat

Eighty-nine taxa were recorded from the 162 plots sampled in 1995 (see Appendix 1). Shrubs were the most common growth form (41 spp.) followed by graminoids (21 spp.), forbs (13 spp.), grasses and trees (5 spp. each) and ferns (4 spp.). Among all growth forms, 19 species were killed by fire and 70 were recorded as resprouting. Of those species killed by fire, only *Banksia marginata* had canopy-held seed banks.

Ordination of sample sites in two dimensions showed distinct clustering of sites in relation to time-since-fire and physiography (Fig. 1). The strongest effects were time-since-fire with 15 years at the top of the ordination and the more recently burnt sites at the base, whilst the drier edge site to the wetter channel sites are distributed left to right (Fig. 1). This floristic gradient is initially wide in the short time-since fire sites but converges with longer time-since fire (Fig. 1). Both light and soil resources were related strongly to physiographic position and time-since-fire (Fig. 1) and when examined using univariate analyses they show the effect of canopy closure on light levels (Table 1, Fig. 2). Univariate analyses also show a strong resource gradient with soil conductivity being higher along the channels with corresponding lower pH (Fig. 2). Both conductivity and pH were, however, not consistently related to time-since-fire (Table 1, Fig. 2).

There was significant negative correlation between conductivity and species richness (r = - 0.53, $P < 0.001$) (Fig. 3). The relationship between species richness, fire response and growth form groups were further examined using GLM which showed inconsistent patterns of time-since-fire and habitats with a significant interaction term (Table 2). The drier outer edge plots contained a greater
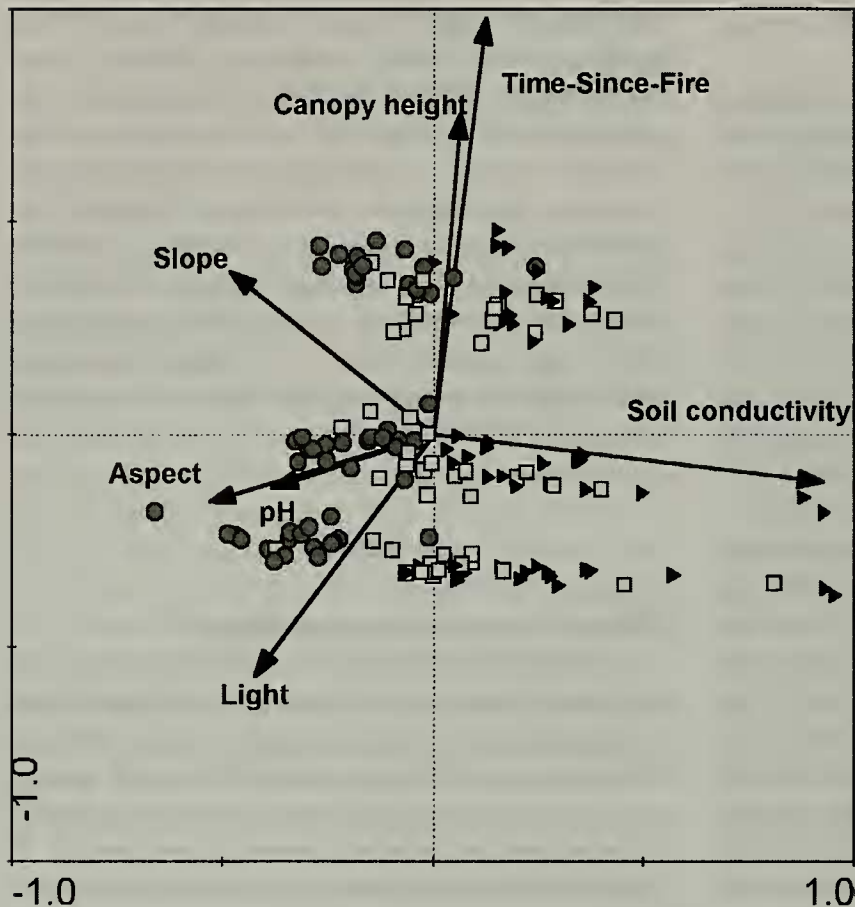
Figure 1. Biplot from the canonical correspondence analysis. Symbols represent plots, arrows represent environmental gradients. Top cluster = 15 year old plots, middle cluster 5 year old, bottom cluster 0.5 year old plots. Circles = edge plots, squares = mid slopes, triangles = drainage channel plots.

and *Lepidosperma limicola* remained the most abundant, but the grass *Amphipogon strictus* was replaced by the obligate seeding twiner, *Cassytha glabella*. The recently burnt edge plots contained a total of 62 species whilst 48 species were documented in plots unburnt for 15 years. In these edge plots the mean number of obligate seeding species and resprouting species decreased over time, as did richness of herbaceous species (Fig. 4).

The mid slope and channel plots in recently burnt sedge-heaths contained a total of 40 species. The most abundant species in the wetter mid slope and channel plots of recently burnt sedge-heaths were *Lepidosperma limicola*, *Baeckea omissa*, *Gymnoschoenus sphaerocephalus* and *Drosera binata*. *Lepidosperma limicola*, *Baeckea omissa* and *Gymnoschoenus sphaerocephalus* were also the most abundant species in the sedge-heaths unburnt for 15 years. By this stage the herb, *Drosera binata,* was much less abundant and was replaced by *Epacris obtusifolia*, an obligate seeder subshrub. In the channel plots resprouter richness decreased through time whilst obligate seeder richness increased (Fig. 4b,c). On the bog slopes species richness appeared to peak six years after fire then decline mainly due to the decrease in grass and sedge species (Fig. 4a,e).

number of species compared with the other plots (Fig. 4a). Species richness declined with time-since-fire in these outer edge plots and reached a peak some five years later on the slopes (Fig. 4a). The four most abundant species in drier edge plots of recently burnt sedge-heaths were *Ptilothrix deusta*, *Amphipogon strictus*, *Leptospermum arachnoides* and *Lepidosperma limicola*. In areas unburnt for 15 years, *Ptilothrix deusta*, *Leptospermum arachnoides*

Effects of fire frequency on shrub species

No significant trend in species composition with fire frequency was detected for shrub species in the CCA analyses, which are shown. Similarly, no effect of fire

Table 1. Summary results for two factor general linear models for time-since-fire and habitat for environmental variables. All models have a Poisson error structures with a log-link function and have scale estimated using Pearson Chi-squared.

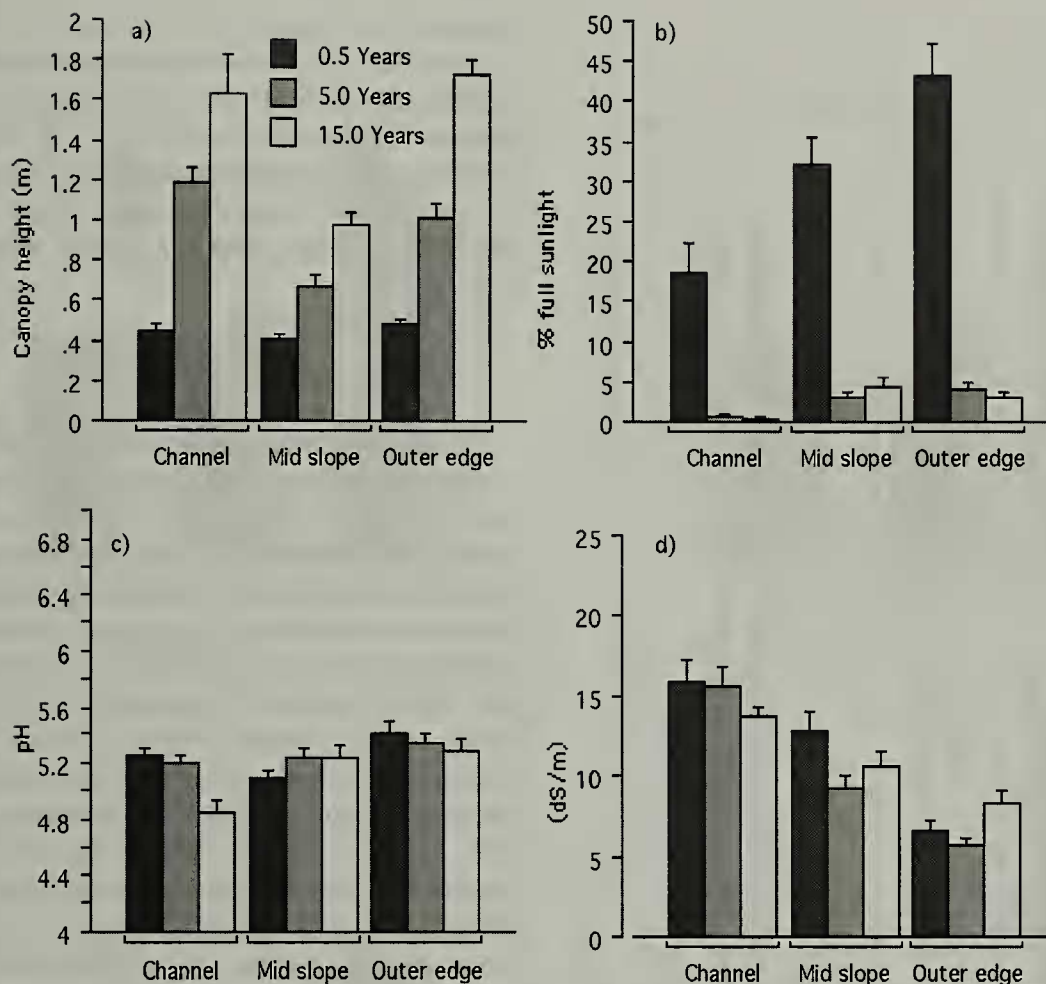| Factor	df	Canopy height		% Light		pH		Conductivity	
		F ratio	*P*	F ratio	*P*	F ratio	*P*	F ratio	*P*
Time-Since-Fire	2	141.7	***	244.9	***	2.9	*	2.6	ns
Habitat	2	30.0	***	27.0	***	8.3	***	65.9	***
TSF x Habitat	4	2.3	ns	2.5	ns	3.7	***	3.3	*
Residual	153								

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Figure 2. Mean (+se) for a) canopy height, b) % full sunlight, c) pH, and d) conductivity for each of three physiographic positions in the sedge-heaths and among three time-since-fire locations.
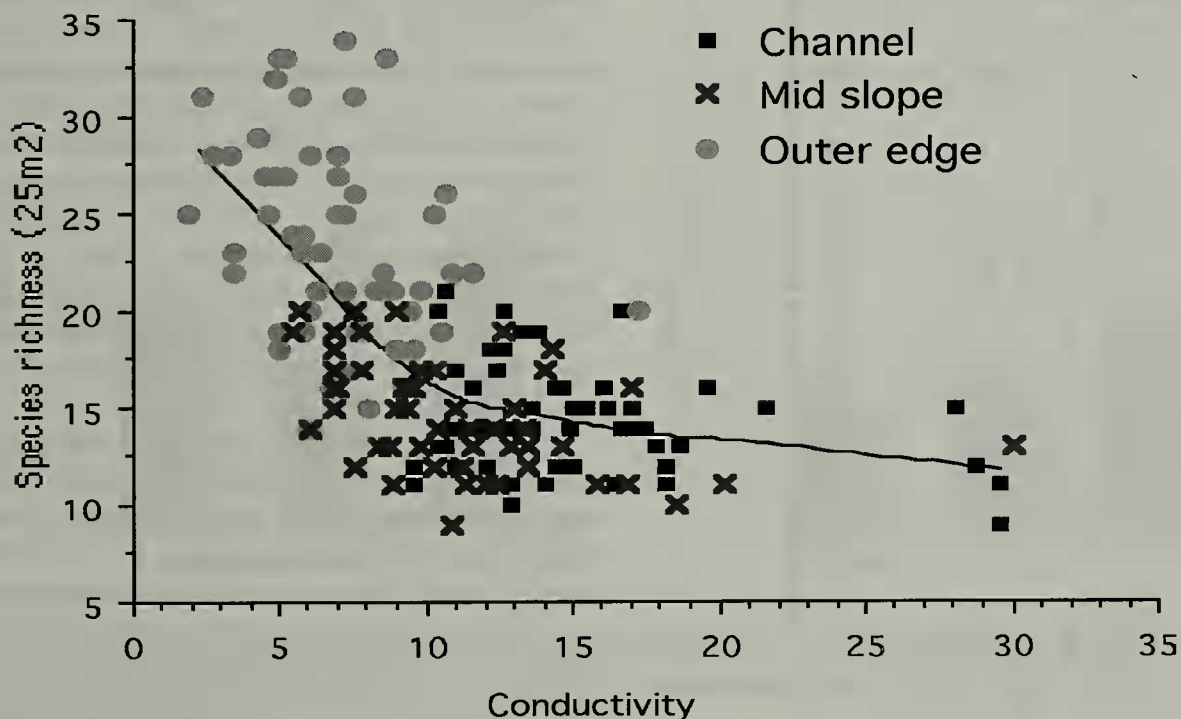

Figure 3. Relationship between conductivity (dS/m), species richness and topographic position across the sedge-heaths at Gibraltar Range. Lowness line fitted.

frequency on species richness was detected (Table 3). However, six common resprouting species had significantly different abundances across sites with different fire frequencies (Table 3, Fig. 5). Of these, *Leptospermum gregarium, Hibbertia rufa, Boronia polygalifolia* and *Grevillea acanthifolia* had lower abundances in sites with the highest fire frequency (Fig. 5).

DISCUSSION

Distinct floristic patterns occur in the sedge-heaths of Gibraltar Range representing both physiographic and fire-regime effects. Firstly, floristic composition varies along gradients in soil moisture, which are linked with increased electrical conductivity and nutrient accumulation along the drainage lines. These drainage-driven patterns are similar to those described by Keith and Myerscough (1993) at Darkes Forest on the southern Sydney plateau of NSW. Despite these structural similarities, major floristic differences separate central and southern NSW from northern regions (Keith 1995; Keith 2004), but more detailed surveys of the sedge-heaths in the Northern Tablelands and comparative analyses are required. Initial comparative analyses of life-history attributes suggest similar growth form composition and fire response syndromes to other east coast heaths (Keith et al. 2002).

Species richness values were generally higher toward the outer edge of the heaths and lower on the slopes and drainage channel corresponding to patterns at Darkes Forest. This inverse relationship between species richness and electrical conductivity (positively correlated with soil fertility) was similar to that found in other heaths (Keith and Myerscough 1993; Myerscough et al. 1996), suggesting a widespread resource-competition effect in heaths with resource gradients. However, the overall number of species encountered was much smaller than the high species richness found in coastal heaths (Keith and Myerscough 1993).

Habitat segregation of serotinous shrub species along gradients of moisture and soil fertility has been explored in manipulative experiments by Williams and Clarke (1997) who suggest that a combination of seedling establishment and seedling survival in relation to moisture gradients segregates species within these sedge-heaths. Patterns of seedling establishment are initiated by fire and the effect of time-since-fire was prominent in our analyses. Following the passage of fire, the sedge-heath canopy is opened up and ground level insolation peaks, but as plants grow taller,

Table 2. Summary results for two factor general linear models for time-since-fire and habitat for functional groups. All models have a Poisson error structures with a log-link function and have scale estimated using Pearson Chi-squared.

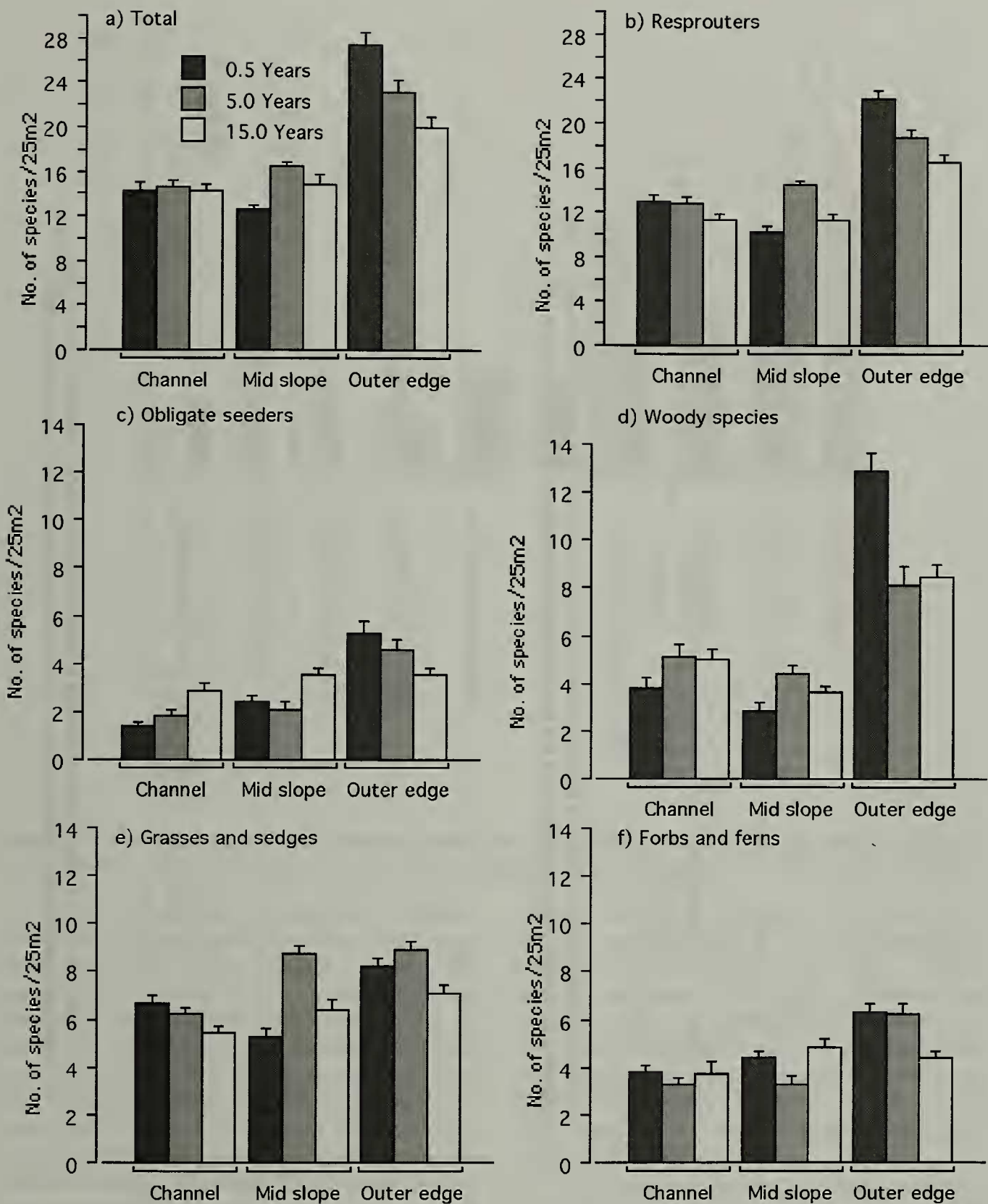| Factor	df	Species richness		Resprouter richness		Obligate seeder richness		Woody richness		Graminoid richness		Grass richness		Forb richness	
		F ratio	P	F ratio	P	F ratio	P	F ratio	P	F ratio	P	F ratio	P	F ratio	P
Time-Since-Fire	2	6.1	**	12.9	***	1.6	ns	2.3	ns	3.1	*	24.3	***	3.6	*
Habitat	2	144.9	***	127.6	***	40.6	***	132.0	***	8.2	***	23.8	***	26.5	***

Figure 4. Mean (+se) for species richness a) total, b) resprouters, c) obligate seeders, d) woody species, e) grasses and sedges, f) forbs and ferns for each of three physiographic positions and among three time-since-fire locations.

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Table 3a. Summary results for linear models for fire frequency and habitat. All models have a Binomial error structures with a logistic link function for species data.

Factor	df	Species richness		Baeckea omissa		Leptospermum gregarium		Hibbertia rufa		Epacris microphylla		Boronia polygalifolia	
		F	P	χ²	P	χ²	P	χ²	P	χ²	P	χ²	P
Fire frequency	2	3.0	ns	2.0	ns	4.8	ns	6.1	*	30.3	***	10.2	***
Habitat	1		***	8.2	**	4.9	*	-	-	-	-	-	-
Fire frequency x Habitat	2	5.2	*	2.0	ns	70.8	***	-	-	-	-	-	-
Residual	30												

Table 3b. Summary results for general linear models for fire frequency and habitat. All models have a Binomial error structures with a logistic link function for species data. Species listed in order of relative abundance.

Factor	df	Leptospermum arachnoides		Banksia marginata (seedlings)		Hibbertia riparia		Grevillea acanthifolia		Hakea microcarpa		Epacris obtusifolia	
		χ²	P	χ²	P	χ²	P	χ²	P	χ²	P	χ²	P
Fire frequency	2	8.5	**	1.1	ns	6.1	*	26.4	**	30.3	***	24.6	***
Residual	30												

* P<0.05
** P<0.01
*** P<0.001

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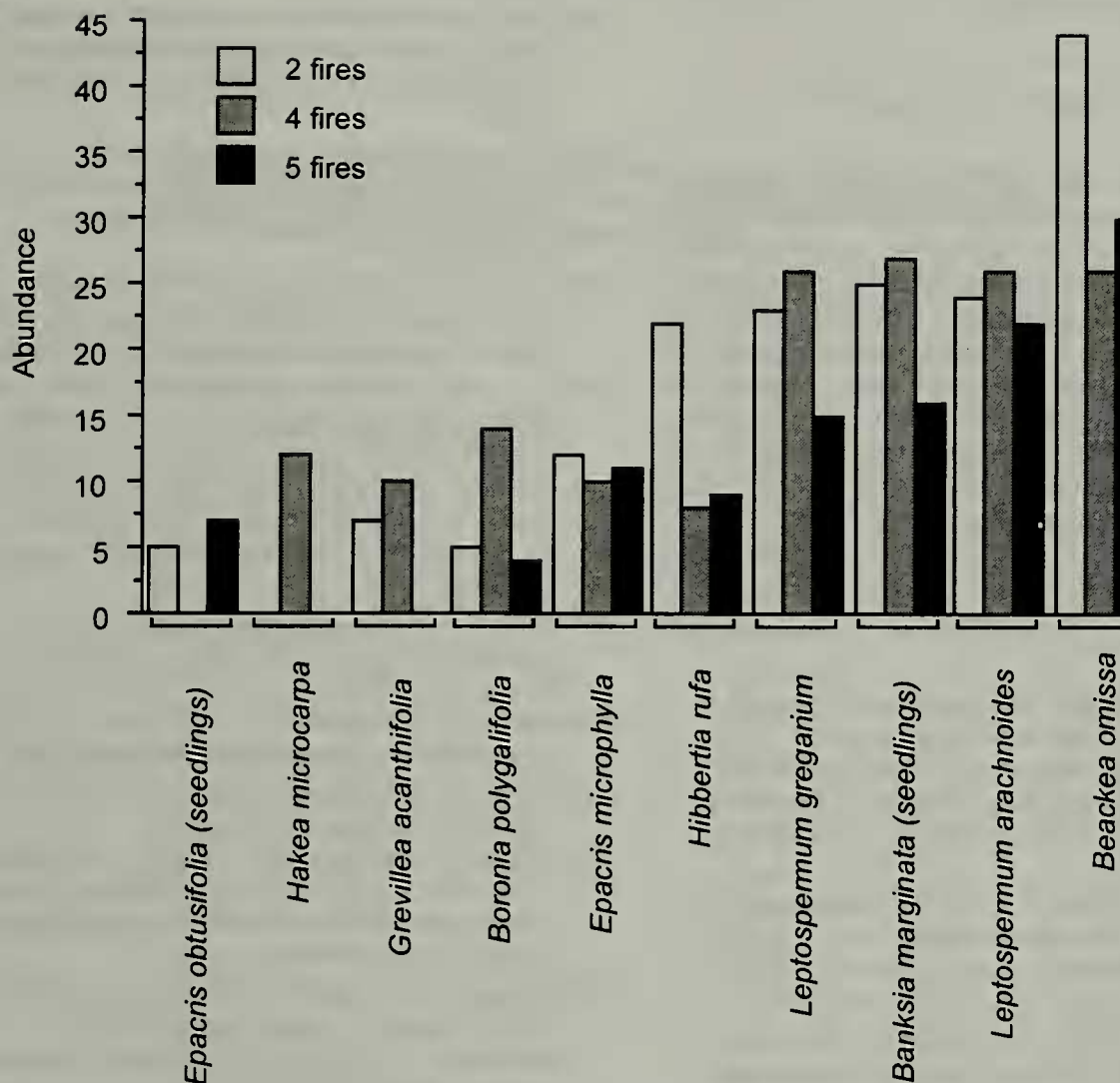Proc. Linn. Soc. N.S.W., 127, 2006

Figure 5. Total abundance scores (frequency score) for the ten most common woody plants recorded in sedge-heaths in 2003, eight months after a fire among areas that been burnt 2, 3, and 5 times since 1964.

ground layer insolation subsequently decreases. Neither soil pH nor conductivity showed consistent trends with time-since-fire although it is likely that post-fire soil nutrients peaked immediately after fire. Hence it is thought that competition for light is the main driver for differences in floristic composition with time-since-fire (Specht and Specht 1989; Keith and Bradstock 1994) or alternatively the differences simply reflect species' life spans. Decreases in woody species richness with time-since fire are prominent in the better-drained, outer-edge heaths. Hence we think that competition rather than variation in the life span of plants is the causal factor.

There were no major decreases in species richness in the channel or slope plots, which may reflect the slower growth dynamics of montane sedge-heaths compared with coastal systems. Overall, variation in floristic composition along the drainage gradient was greatest immediately after fire,

and then became less variable at 15 years time-since-fire. This may reflect the lack of strong competitive exclusion in the drainage channel heaths, possibly due to their narrow and patchy distribution. We think the alternative explanation of the lack of short-lived species immediately after fire unlikely because short-lived species were common along creek banks. Unfortunately, studies of long-unburnt sedge-heaths were halted in 2003 when all long-unburnt sedge-heaths were burnt in wildfires.

Fire frequency appears to have much less influence on composition than time-since-fire, although only shrub data were sampled. When shrub species abundances were examined individually several dominant species had reduced abundances under frequent fire regimes. This is consistent with patterns in the adjacent dry sclerophyll forests (Knox and Clarke in this volume) where higher fire frequencies reduced plant performance. We would

predict, however, that if the intervals between fires were less than eight years then the dominance and composition would change.

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Appendix 1. Species recorded in sample sites of the sedge-heaths in Gibraltar Range National Park, their growth form and fire response. R = resprouting, S = obligate seeding. * exotic

Species name	Growth form	Sprouting
Allocasuarina littoralis	Tree	R
Amphipogon strictus	Grass	R
Aotus subglauca var. *subglauca*	Shrub	R
Aristida ramosa	Grass	R
Austrostipa pubescens	Grass	R
*Axonopus affinis	Grass	R
Baeckea omissa	Shrub	R
Baloskion fimbriatus	Graminoid	R
Baloskion stenocoleus	Graminoid	R
Banksia spinulosa	Shrub	R
Banksia marginata	Shrub	S
Baumea rubiginosa	Graminoid	R
Blandfordia grandiflora	Graminoid	R
Boronia microphylla	Shrub	R
Boronia polygalifolia	Sub-shrub	S
Bossiaea scortechinii	Shrub	R
Brachyloma daphnoides ssp. *glabrum*	Shrub	R
Caesia parviflora	Graminoid	R
Callistemon pallidus	Shrub	R
Callistemon pityoides	Shrub	R
Cassytha glabella	Forb	S
Caustis flexuosa	Graminoid	R
Conospermum taxifolium	Shrub	R
Cryptostylis subulata	Graminoid	R
Dampiera stricta	Forb	R
Dianella caerulea	Graminoid	R
Dillwynia phylicoides	Shrub	R
Drosera binata	Forb	R
Drosera spatulata	Forb	R
Empodisma minus	Graminoid	R
Entolasia stricta	Grass	R
Epacris microphylla var. *microphylla*	Shrub	R
Epacris obtusifolia	Shrub	S
Eucalyptus acaciiformis	Tree	R
Eucalyptus campanulata	Tree	R
Eucalyptus ligustrina	Tree	R
Eucalyptus williamsiana	Tree	R
Euphrasia collina ssp. *paludosa*	Forb	R
Gleichenia dicarpa	Fern	R
Gompholobium sp. "B"	Shrub	R

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Gonocarpus micranthus	Forb	S
Gonocarpus teucrioides	Forb	R
Goodenia bellidifolia	Forb	S
Goodenia hederacea	Forb	S
Grevillea acanthifolia ssp. *stenomera*	Shrub	R
Grevillea acerata	Shrub	R
Gymnoschoenus sphaerocephalus	Graminoid	R
Hakea laevipes ssp. *graniticola*	Shrub	R
Hakea microcarpa	Shrub	R
Hibbertia rufa	Shrub	R
Hibbertia riparia	Shrub	R
Hovea heterophylla	Sub-shrub	R
Hybanthus monopetalus	Forb	S
Hypericum japonicum	Forb	S
Isopogon petiolaris	Shrub	R
Kunzea bracteolata	Shrub	S
Lepidosperma limicola	Graminoid	R
Lepidosperma tortuosum	Graminoid	R
Leptospermum arachnoides	Shrub	R
Leptospermum brevipes	Shrub	R
Leptospermum gregarium	Shrub	R
Leptospermum novae-angliae	Shrub	R
Lepyrodia anarthria	Graminoid	R
Lepyrodia scariosa	Graminoid	R
Lindsaea linearis	Fern	R
Logania pusilla	Sub-shrub	R
Lomandra elongata	Graminoid	R
Lomandra longifolia	Graminoid	R
Lycopodium sp.	Fern	S
Melichrus procumbens	Shrub	R
Mirbelia rubiifolia	Shrub	R
Monotoca scoparia	Shrub	R
Patersonia sericea	Graminoid	R
Persoonia rufa	Shrub	S
Petrophila canescens	Shrub	R
Phyllota phylicoides	Shrub	R
Pimelea linifolia ssp *collina*	Shrub	S
Platysace ericoides	Shrub	S
Ptilothrix deusta	Graminoid	R
Pultenaea polifolia	Shrub	S
Pultenaea pycnocephala	Shrub	S
Rhytidosporum diosmoides	Sub-shrub	S
Schizaea bifida	Fern	R
Schoenus sp.	Graminoid	R
Sphaerolobium vimineum	Shrub	R
Sprengelia incarnata	Shrub	S
Thysanotus tuberosus	Graminoid	R
Trachymene incisa ssp. *incisa*	Forb	R
Xanthorrhoea johnsonii	Graminoid	R
Xyris operculata	Graminoid	R

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